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Influence of Massive and Long Distance Migration on Parasite Epidemiology: Lessons from the Great Wildebeest Migration

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Abstract: Very little is known about the influence of massive and long distance migration on parasite epidemiology. Migration can simultaneously minimize exposure to common parasites in their habitats and increase exposure to novel pathogens from new environments and habitats encountered during migration, while physiological stress during long distance movement can lead to immune suppression, which makes migrants vulnerable to parasites. In this paper, we investigated the diversity, prevalence, parasite load, co-infection patterns and predilection sites of adult gastrointestinal helminths in 130 migrating wildebeests and tested for their relation with animal age, sex and migration time (which also could indicate different migration routes), and compared them with the non-migratory wildebeest. Surprisingly, only four parasite species were found, *Oesophagostomum columbianum*, *Haemonchus placei*, *Calicophoron raja* and *Moniezia expansa*, which were lower than in non-migratory wildebeest reported in the literature. These parasites were generalists, infecting livestock, and suggests that wildebeest and livestock, because of their interaction during migration, have a crossinfection risk. There was a negative relation between parasites diversity, prevalence and intensity of infection, and host age, which suggests that wildebeests acquire protective immunity against these parasites as they get older. Prevalence and intensity of infection were higher among wildebeest crossing the Mara Bridge (early migrants) compared to those crossing the Serena (late migrants), which suggests that early migrants (or migrants originating from different areas) have varying infection intensities. The prevalence and intensity of infection were higher in males compared to females and may be due to ecological, behavioural, or physiological differences between males and females. Our findings compared to those of previous studies suggest that migration may provide a mechanism to minimize exposure of hosts to common parasites through migratory escape, but this result awaits examination of helminths epidemiology of nonmigratory wildebeests from areas of migrant origins. The potential parasitic cross-infection between wildebeests and livestock is a real risk to be taken into account in the management of wildebeest migration corridors.

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ABBREVIATIONS

MMNP Masai mara national reserve

GIT Gastro-intestinal tract

GLM General linear model

KWS Kenya wildlife service

INTRODUCTION

Long distance migration, common in several species of birds, butterflies and mammals can affect the diversity, prevalence, and burden of parasites and pathogens in migratory populations of these species. Parasites epidemiology of migrant animals is of pivotal interest, nonetheless very little is known regarding parasite prevalence and diversity in migratory populations of many mammalian species, including the blue wildebeest (*Connochaetes taurinus*), a bovid species known to migrate annually from the Serengeti in Tanzania to Masai Mara in Kenya covering approximately 3000 km in search of adequate pasture and water.

Long distance migration is speculated to have both negative and positive influences on pathogen transmission, diversity, prevalence and parasite burden/load within migrants depending on host migratory behaviour and pathogen

traits (Altizer et al. 2011). In terms of the negative consequences of long distance migration, migrants may come into contact with different habitats with different parasite faunas and hosts species (Altizer et al. 2011). Migrants are particularly likely to acquire new environmentally transmitted parasites such as gastro-intestinal helminths, whose prevailing mode of transmission is the oral faecal route. In addition, the energetic demands of migration can compromise host immunity, enhancing susceptibility to infection and intensifying the impacts of disease. Long distance migration is energetically costly, and many wildebeest die from physical exhaustion, drown as they cross the Mara River and are attacked by predatory crocodiles. Like in other vertebrate species, such physical exhaustion during migration is physiologically stressful, and migration-induced stress may cause immune suppression thereby increasing infection risk with different parasites and pathogens.

Theoretical model predictions suggests that long distance migration can reduce disease prevalence through migratory escape from parasite invested areas and selective mortality on parasitized individuals during migration (Avgar et al. 2013; Johns and Shaw 2016). There is increasing empirical support for these theoretical predictions; long distance migration may enhance avoidance of parasite, even the selection of parasite-free habitats, as suggested in shorebirds (Piersma 1997) and reindeer (Folstad et al. 1991). The parasite fauna of non-migratory wildebeest is well documented (Horak et al. 1983) but nothing is known about the parasites of migratory wildebeest. Parasite interactions and co-infections may also affect the host's immune response leading to immune suppression or cross-reactive immune responses (Pedersen and Fenton 2007; Cobey and Lipsitch 2013). Currently, insights into host-parasite interactions are still largely based on studies involving single parasite species infecting single hosts. Yet, in the real world, hosts are often infected by numerous parasite genotypes of the same or different species simultaneously (Ulrich and Schmid-Hempel 2012). Since migratory wildebeests are likely to harbour multiple helminth infections and fresh carcasses were available from annual natural deaths, they provided an opportunity to investigate the epidemiology of the most common gastrointestinal parasites and parasite predilection and co-infection patterns within hosts. These patterns may help reveal parasite interactions like competition for host resources or attachment sites within the host (Cattadori et al. 2007; Mideo 2009) or interactions between parasites and the host's immune system. The literature that deals directly

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with the distribution of helminths in the gastrointestinal tract of vertebrates is relatively limited (Crompton 1973). Studies on parasite co-infection have mainly focused on exposure risk factors and little attention has been given to patterns of parasite predilection sites within hosts and its relationships with patterns of co-infection since this may reveal aspects of parasite ecology such as competition for attachment sites or resources within host species (Cattadori et al. 2007; Mideo 2009). Interactions between parasites may be indirectly manifested via the host's immune suppression by one parasite benefiting another (Graham 2008; Fenton and Perkins 2010; Telfer et al. 2010; Hawley and

Altizer 2011).

This study aims to (1) evaluate the parasite diversity, and prevalence and intensity of infection of adult helminths in migratory wildebeests, (2) test the influence of host age, sex and migration time (which could also mean different migration routes) on helminth diversity, and prevalence and intensity of infection, (3) determine the co-infection patterns, (4) determine the predilection sites of helminths in the gastrointestinal tract of the wildebeests, and (5) assess the general putative influence of massive and long distance migration on parasite epidemiology.

MATERIALS AND METHODS

Study Area

The study was conducted in the Masai Mara National Reserve (MMNR) located in southwest Kenya along the Kenya-Tanzania border (1°10'000 and 2°10'000S, 34°14'500 and 36°10'000E). MMNR occupies an area of approximately 1510 square Kilometers and has a high density of wildlife populations including large mammals such as African elephants, lions, leopards, African buffaloes, black rhinoceros, wildebeests and several antelope species (Mijele et al. 2013). The reserve is contiguous with the Serengeti National Park on the Tanzanian side and is traversed by the Mara River flowing from the Mau escarpments across the reserve into Serengeti and drains in Lake Victoria. The MMNR and Serengeti form part of the blue wildebeests' migration route. Wildebeest migrating into the Mara use three major crossing areas: Mara Bridge (where the early migrant wildebeest cross the river), Serena (where the late migrants cross the river) and Governors (Fig. 1).

Post-Mortem Procedures and Parasite Sampling

Post-mortem examination was carried out on 130 migratory wildebeests that drowned along the Mara River between 2010 and 2012 at two different locations along the Mara River (Fig. 1). Sex, age and species and number of gastrointestinal parasites were recorded from all wildebeest that were dissected. This sample had 66 adults, 13 subadults, and 51 juveniles, comprising 65 females and 65 males. Wildebeest carcasses were retrieved from the river using an anchor attached to a rope. Each carcass was put on dorsal recumbence and cut open on the ventral part of the abdomen along the linea alba to access the abdominal contents. Once the abdomen was opened, prestomachs, abomasum, small and large intestines were ligated at omaso-abomasal, abomaso-duodenal and ileo-caecal junctions to prevent parasites spilling from one part to another. The ligated gastrointestinal tracts were processed for helminth recovery as described by Horak et al. (1982). Specifically, contents from each section of the gastro-intestinal tract were washed through a sieve 0.5 mm. All material that was not washed was first examined by eye and all visible adult worms were isolated and counted. Secondly, we examined all the contents using a hand held 910 magnifying glass and all tiny worms were picked and isolated from each section of the gastrointestinal tract. Worms were first classified based on gross morphology and then counted. Several worm samples were collected into tubes according to the site in the gastrointestinal tracts it was collected from and according to our field ID. Worm samples were preserved in 70% ethanol in the field and a representative sample of this field collection based on our

field IDs and predilection sites were sent for identification at Meguro Parasitological Museum, Japan.

Age Estimation of Wildebeest Carcasses

The age at death of wildebeest was estimated based on horn length and shape, body size and pelage colour and tooth wear. Detailed relationships between horn length and shape and wildebeest age are described in Talbot and Talbot (1963) and a detailed description of assigning age based on tooth wear patterns is available elsewhere (Attwell 1980). Juveniles were classified as animals 1 year or less; subadults were classified as animals between 1 and 2.5 years of age. Animals above 2.5 years were classified as adults.

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Figure 1. Map of Masai Mara National Reserve and associated protected areas.

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Morphological Identification of Parasites and Species Diversity

In the lab, the parasite samples were washed in water overnight in order to remove the fixative, relax internal organs and enhance clear examination of internal organs on a microscope. The cestodes and trematodes were then placed between two glass slides tightened by cotton thread and left to flatten in 50% acetic acid for 1 week, to about 1 mm thick. The cestodes were stained by alum carmine, dehydrated in ethanol, cleared by xylene and mounted by Canada balsam. The trematodes were unstained and cleared by glycerine. The nematodes were directly cleared by glycerine. All specimens were observed and identified at 50–400 magnification under a light microscope.

Statistical Analysis

Influence of Host Sex, Age and Migration Time (and the Interaction Between these Factors) on Prevalence and Intensity of Infection and Diversity of Adult Gastro-Intestinal Parasites

Fisher Exact test was used to determine the associations between prevalence of infection and animal sex, age and migration time.

A generalized linear model with a Poisson family and an identity link function was used to test the hypothesis that age, sex and migration time (represented by location of entry into the Mara National Reserve), or any interaction between these factors are important predictors of gastrointestinal helminths infection intensity. We used the total count of adult parasites of each species (or all species total counts combined) as a dependent variable.

In the case of parasite diversity, we used a proportional odds ordinal logistic regression model, where the number of parasite species (parasite diversity) by wildebeest was used as a dependent variable. The final and best model was selected based on AIC and these are the models reported in the results.

Predilection Sites of Adult Gastrointestinal Helminths

We examined the presence and co-infection possibility of common helminth parasite species in the various parts of the gastrointestinal tract. For testing this association, we used a χ^2 test.

All statistical analyses were performed using R software version 3.2.0 (R Core Team 2014).

RESULTS

Parasite Species Identification and Diversity

Four species (a cestode, a trematode and two nematodes)

were identified in the studied wildebeests. The single cestode belonged to the genus *Moniezia* of the family Anoplocephalidae (Beveridge 1994). From the arrangement of interproglottidal glands (Schmidt 1986), this cestode was classified as *Moniezia expansa* (Fig. S1a, b).

The trematode belonged to the genus *Calicophoron* of the family Paramphistomidae (Jones 2005). We observed small tegumental papillae arranged densely around the genital atrium, that is typical of *Calicophoron raja* (Eduardo 1983). The body length was approximately 7 mm and egg size was 145–150 μm , consistent with the description of this species (Fig. S1c–e).

Based on the structure of head and uterus, one of the nematodes was found to belong to the genus *Oesophagostomum* of the family Chabertiidae (Lichtenfels 1980).

According to key to the species (Popova 1958), this nematode was identified as *O. columbianum* (Fig. S1f–h). Body length of this sample was 12.3–13.9 mm in males and 16.8–20.1 mm in females. The number of outer/inner crowns in head was about 20/40. Spicule length was 752–886 μm . Distance from vulva to tail end was 1.22–1.39 mm. The whole body size, lengths of spicules and position of vulva are coincident with the description of this species.

The other nematode belonged to the genus *Haemonchus* of the family Trichostrongylidae (Durette-Desset 1983), based on the structure of bursa and spicules of the male. The morphological measurements of our samples were consistent with the description for *H. placei*. Body length was 13.1–13.7 mm in the males and 22.5–22.8 mm in females. The right and left spicule length were 465–467, and 466–473 μm long, respectively (Fig. S1i, j). Gubernaculum length was 224–232 μm and the distance from vulva to tail end in a female was 4.12–4.28 mm. In addition, according to Lichtenfels et al. (1994), who studied the morphology of *H. contortus* and related species, the present nematode fits *Haemonchus placei* description, because of the number of cuticular ridges or synlophe (34 in *H. placei* 712 D. Mijele et al.

_34), extending posteriorly only to the end of the anterior quarter of the body.

Predilection Sites of Adult Gastrointestinal Helminths

Chi square tests analyses revealed significant associations between parasite species presence with distinct sections of the gastrointestinal tract (Fig. S2). *M. expansa* was significantly more present in the small intestines ($\chi^2 = 90.93$, $\text{df} = 5$, $P < 0.001$), while *O. columbianum* was significantly more in the large intestines ($\chi^2 = 275.58$, $\text{df} = 5$, $P < 0.001$) than any other section of the gastro-intestinal tract. *H. placei* was more frequently found in the abomasum than in any other part of the gastro-intestinal tract ($\chi^2 = 95.31$, $\text{df} = 5$, $P < 0.001$). *C. raja* was predominantly found in the rumen ($\chi^2 = 5.03$, $\text{df} = 5$, $P = 0.4127$). There was no significant overlap in terms of predilection sites among the common parasites encountered in wildebeest (Fig. S2).

Helminths Prevalence, Intensity and Co-infection

Seventy two percent (94/130) of the wildebeests sampled were positive for one or more of the aforementioned major gastro-intestinal parasites. Males were more frequently affected, 80% (52/65), than females, 64.62% (42/65), and the

difference was statistically significant ($P = 0.023$). Young animals (1–5 years old) were more frequently infected (83.82%), than old animals (6–10 years old) (58.18%), and this result was also statistically supported ($P = 0.002$).

Wildebeest crossing through Mara Bridge had higher prevalence of helminth infections (86.67%, 13/15) than those crossing through Serena (70.43%, 81/115); however the difference was not statistically supported.

Table 1. Selected GLM Models Based on AIC for Predicting Intensity of Infection for All Parasites (Total Parasite Load), *Haemonchus*

placei, *Moniezia expansa*, *Oesophagostomum columbianum* and *Calicophoron raja* Using Crossing Area (Representing Migration Time, or

Different Migration Routes), Age and Sex of the Wildebeest as Explanatory Variables in the Different Models.

Parasite load Estimate Std. error Z-value Pr ($>|z|$) Null deviance df1 Residual deviance

df2 AIC Explained

deviance

Total load of parasite 3672.2 122 2283 119 2588.6 0.3783

(Intercept) 3.907 0.079 49.532 $<2e-16$

Crossing area -2.296 0.061 -37.689 $<2e-16$

Age 0.396 0.066 5.979 0.000

Sex -0.031 0.010 -3.195 0.001

Haemonchus placei 146.91 122 130.73 119 138.73 0.1101

(Intercept) 0.697 0.836 0.834 0.404

Crossing area -1.174 0.740 -1.588 0.112

Age -0.223 0.075 -2.995 0.003

Sex 0.497 0.438 1.136 0.256

Moniezia expansa 102.412 122 73.603 119 81.603 0.2813

(Intercept) -16.273 1924.553 -0.008 0.993

Crossing area 16.685 1924.553 0.009 0.993

Age -0.756 0.299 -2.528 0.012

Sex -0.718 0.574 -1.251 0.211

Oesophagostomum columbianum 170.12 122 167.08 119 175.08 0.0179

(Intercept) 0.538 0.780 0.690 0.490

Crossing area -0.315 0.711 -0.443 0.658

Age -0.091 0.057 -1.606 0.108

Sex 0.042 0.375 0.113 0.910

Calicophoron raja 124.200 122 89.104 119 97.104 0.2826

(Intercept) -1.965 0.979 -2.007 0.045

Crossing area -2.538 0.940 -2.701 0.007

Age 0.455 0.106 4.284 0.000

Sex 0.786 0.548 1.434 0.152

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The prevalence of adult gastrointestinal helminths in wildebeest was high for *O. columbianum* at 46.2% ($n = 60$) and lower for *H. placei* at 29.2% ($n = 38$), *C. raja* 20% ($n = 26$) and *M. expansa* 14.6% ($n = 19$). Parasite load (worm burden) was variable among infected wildebeests (range: 1–271 adult parasites). The mean \pm (SD) and median worm burden were $13 \pm (34)$, and four worms per individual host, respectively.

The prevalence of single infections was 38.46%. The prevalence of concurrent infections with two, three and four parasites was 26.15, 5.38 and 2.31%, respectively, while 27.69% of the wildebeests were not infected by any adult helminths. Concurrent infection of hosts with two, three or four parasites was not significantly different from random expectation ($\chi^2 = 6.019$, $df = 3$, $P = 0.111$).

Intensity of Infection with Adult Helminths in

Relation to Host Sex, Age and Crossing Time

When dealing with each parasite species separately, the best model based on AIC number, revealed that there was a notable effect of age on intensity of infection for most parasites in wildebeests (Table 1). The infection of *H. placei*, and *M. expansa* was significantly higher in young animals (<2 years

old) compared to adult wildebeests (>3 years old), but intensity of infection with *C. raja* was higher in adult wildebeest, compared to the young ones. Migration time (Crossing Area) was also significant, with wildebeest crossing through Mara Bridge having a higher intensity of infection than Serena.

However, there was no effect of age, sex and migration time on the infection for *O. columbianum* (Table 1).

Figure 2. The influence of sex, age (in years) and wildebeest crossing area (representing migration time and/or different migration routes) on

adult infection intensity in migratory wildebeests.

Table 2. Coefficients of Logistic Regression Model and Intercepts for Each Level of Ordered Response Showing the Variation in Number of Parasite Species Infecting Wildebeests.

Variables Coefficients Std. error t value P value

Age -0.1301 0.0532 -2.448 0.0144

Sex (male vs female) 0.2956 0.34 0.8694 0.3846

Area crossing (serena vs mara) -1.2818 0.6546 -1.958 0.0502

Intercepts

0|1 -2.6048 0.7417 -3.5118 0.0004

1|2 -0.8646 0.7108 -1.2164 0.2238

2|3 0.9618 0.7385 1.3022 0.1928

3|4 2.2565 0.8718 2.5884 0.0096

Statistically significant P values are shown in italics

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The best Generalized Linear models, based on AIC number, revealed that infection for all parasites combined was higher in juveniles compared to adults and sub-adults. In addition, wildebeests crossing through the Mara bridge had higher infection than wildebeests crossing from Serena, and males were more infected compared to females (Fig. 2). The final models did not include any interactions between variables.

Diversity of Adult Gastro-Intestinal Helminths in Relation to Host Sex, Age and Crossing Time

A proportional odds logistic regression model fitted to an ordered factor response (number of parasite species) revealed that the number of parasite species in a wildebeest was predicted by animal age and migration time (Table 2). The younger the animal, the more parasite species it harboured (Fig. 3). Wildebeests sampled from Serena had higher parasite diversity than wildebeests crossing from Mara Bridge (Fig. 2).

DISCUSSION

Parasite Predilection Sites and Co-infection

Adult parasites recovered from the wildebeests occupied different parts of the gastrointestinal tract with no overlap in predilection sites among parasites. Predilection sites are largely consistent with similar parasites in domestic animals (Sutherland and Scott 2009; Roeber et al. 2013).

Co-infections among the four common wildebeest parasites were random association. This result was expected given that the common parasites do not compete for predilection sites in the hosts. Numerous experimental studies have investigated and confirmed the existence of negative and synergistic interactions among parasites (Kloosterman et al. 1984, 1990; Kloosterman and Frankena 1988; Dobson et al. 1992; Dobson and Barnes 1995; Ploeger et al. 1995), but there is little empirical evidence to suggest that these interactions occur in the wild.

Figure 3. Probability of infection with different species of helminthes as a function of age in wildebeests.

X animal ages (years), and the

short lines at the x-axes represent the number of studied animals from each age class. Y Probability of being infected. Sub-panels show increasing parasite diversity ranging from 0 (no infection) to 4 parasite species.

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Gastrointestinal Helminths Diversity

The diversity of the adult helminths infecting migratory wildebeests was surprisingly low, and the four identified species were just a subset of the larger number infecting non-migratory blue wildebeests in South Africa (Horak et al. 1983; Junker et al. 2014). The apparently low diversity could be an artefact of not sampling micro-parasites, or mirror differences in ecology between the Masai Mara-Serengeti ecosystem where migrants were sampled, and South Africa where most studies of non-migratory wildebeest have been conducted. However, when we compared gastrointestinal macro-parasites detectable by visual inspection in non-migratory wildebeests in Kruger National Park, they had a higher parasite diversity consisting of 12 species from 7 genera (Horak et al. 1983). The low diversity of parasites in migratory wildebeests observed in this study is consistent with the hypothesis that migration helps in escaping parasite build up, as observed in other migratory mammals (Hausfater and Meade 1982; Folstad et al. 1991). Further studies of parasite diversity of local sympatric wildebeests are needed to definitively answer the question of whether the long distance wildebeest migration is beneficial to hosts in terms parasite avoidance. All four helminths recovered from the gastrointestinal tract of the migratory wildebeests had relatively low infection intensities and, quite surprisingly, were generalist species that commonly infect livestock (Dube et al. 2004; Tariq et al. 2008). Helminths recovered from migrating wildebeest in this study could result from cross-infection from the domestic reservoirs along pastoral landscapes that dominate the wildebeest migratory routes (Dash 1973; Nwosu et al. 1996, Lone et al. 2011; Junker et al. 2014). The relative rarity of *C. raja* may be related to the scarcity of swampy areas required for the survival of intermediate snail host on the migratory pathways of wildebeest. *O. columbianum* and *H. placei* were the most prevalent parasites in the studied wildebeests signifying their importance in the Masai Mara—Serengeti wildlife areas or in migratory wildebeests. In general, we observed higher parasite diversity in younger wildebeests compared to older wildebeests. The decrease in parasite diversity in older individuals is well documented in helminths, and is deemed driven by the immune response elicited by repeated infections (Galvani 2005; Mutapi et al. 2008). These results contrasts with findings in other host taxa where parasite diversity is positively correlated to the age (Lo et al. 1998), suggesting that immunity and not exposure is limiting parasite infection patterns (Baird 1998; Peyerl-Hoffmann et al. 2001).

Effect of Age on Gastrointestinal Helminths Prevalence and Intensity of Infection

The prevalence and intensity of infection with *H. placei*, and *M. expansa* was higher in juveniles than in sub-adults or adults. In livestock, juveniles are well known for less

efficient protective immunity than adults against *H. placei* and *M. expansa*, due to their limited exposure to these parasites (Kloosterman et al. 1991; Ploeger et al. 1995). However, *C. raja* was significantly more prevalent in older animals compared with younger ones, as already reported for paramphistomes in African cattle (Pfukenyi et al. 2005). It suggests that wildebeests do not particularly invest in immunity development to this parasite, and that older animals had simply more opportunities to encounter this long-lived parasite than young individuals.

Effect of Migration Time (or Different Migration Routes) on Parasites Infection Prevalence and Intensity

Interestingly, the wildebeests arriving earlier or crossing through Mara Bridge had higher prevalence and intensity of infection than those arriving later to the Serena. This result suggests that either (1) early migrants originate from locations or use routes with a richer environmental parasitic infestation than late migrants, or (2) early migration is undertaken by individuals which are suffering from greater nutritional stress, in their areas of origin compared with late migrants (Holdo et al. 2009), and are therefore more vulnerable to parasite infection.

Effect of Sex on Parasites Infection Prevalence and Intensity

The sex of the hosts was important factor influencing the prevalence and intensity of helminth infection males were highly infected compared with females, in concordance with several studies report on sex-biased differences, loads/burden, with males of many host species exhibiting higher parasitism than females (Poulin 1996). A sex bias in parasitism may be due to ecological, behavioural, or physiological differences between males and females (Zuk and McKean 1996). Specifically, males have higher levels of 716 D. Mijele et al.

testosterone than females and testosterone is known to have immunosuppressive effects. In many polygynous species, males range widely than females, and such ranging behaviour can also expose males to heavier parasitic challenge (Zuk and McKean 1996).

CONCLUSION

The parasite species infecting migratory wildebeests are remarkably fewer than those found in non-migratory wildebeest (reported by previous studies) suggesting that long distance and massive migration is beneficial as a mechanism of parasite avoidance. Notwithstanding, due to the potential nutritional stress, migration could make early migrant wildebeests more prone to parasite infection. Most parasites recovered from migrating wildebeests were generalist parasites known to infect livestock, which is evidence of cross-infection along the migration routes. This result suggests that maintaining migration corridors for wildebeest free from livestock grazing may be wise policy in maintaining long-term health and conservation of both livestock and wildebeest, especially the most vulnerable young ones.

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AUTHORS' CONTRIBUTIONS

DM, PC, MO, SA, and TI conceived and designed the experiments for the paper. DM, PC, VO, LR, RCS, LR, RCS, SA have been involved in drafting the manuscript or revising it critically for important intellectual content. Manuscript was analyzed, discussed and written by all co-authors. All authors read and approved the final manuscript.

COMPLIANCE WITH ETHICAL STANDARDS

CONFLICT OF INTEREST The authors declare that there were no competing interests.

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